COMPARATIVE FORAGING ECOLOGY OF
LOUISIANA AND NORTHERN WATERTHRUSHES

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Closely related and ecologically similar species have been the focus of many recent studies on the behavior and ecology of birds. Such studies have investigated the possibility of interspecific competition and conditions that might act to reduce competition (MacArthur 1972, Cody 1974). Conditions considered include differences in foraging zones and methods (MacArthur 1958; Morse 1967, 1971), microhabitat selection (Wiens 1969), interspecific territoriality (Miller 1968, Rice 1978), character displacement (Abbott et al. 1977), contiguous allopatry (Diamond 1970, Terborgh and Weske 1975), and preferences for size and type of food (Hespenheide 1975).

Wiens (1977) pointed out that the mere existence of interspecific differences may not adequately explain the ability of species to coexist, because the differences could have evolved in response to selective forces other than competition. Furthermore, interspecific competition may not be selectively important in variable environments, where populations are often below equilibrium densities. The use of measures of niche overlap to assess the intensity of competition has also been criticized in situations of unlimited resources (e.g., Pianka 1976, Abrams 1980).

However, in a review of studies of competition, Schoener (1982) noted that even in variable environments periods of limited resources may often occur. Species demonstrated to have high niche overlap and low amounts of competition may even verify the importance of interspecific competition. He hypothesized that similar species converge in using superabundant resources, for which competition would be unnecessary, and diverge in using limited resources, for which competition would be great.

I have studied sympatric populations of the ecologically and morphologically similar Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes to determine whether their feeding behavior and prey availability in their territories indicate the occurrence of interspecific competition. Foraging of other wood warblers (Parulinae) has been studied extensively by MacArthur (1958), Rabenold (1978), and Morse (1980), but except for the Ovenbird (*S. aurocapillus*; Zach and Falls 1978), studies of *Seiurus* spp. have been largely qualitative (Bent 1953; Eaton 1957, 1958). Bent (1953) and Eaton (1957, 1958) reported that the insectivorous waterthrushes, though primarily terrestrial and as-
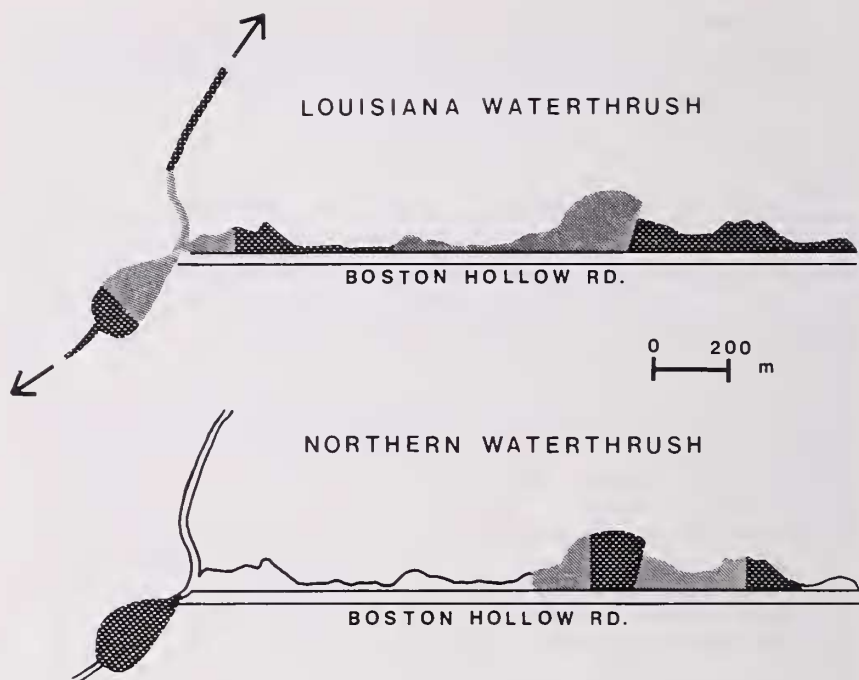
FIG. 1. Distribution of waterthrush territories at Boston Hollow, 1980. Width of swamp equals scale × 2; dark and light stipple patterns denote shapes of adjacent territories.

sociated with wetlands, can feed in leaf litter, water, foliage, and on flying insects.

STUDY AREAS AND METHODS

Habitats. — I studied adult waterthrushes in northeastern Connecticut from early April to mid-August, 1978–1980. Despite Bent's (1953) report that the species only rarely share the same site, my 9 years of observations in Connecticut indicate that they regularly breed near each other.

My principal study site, Boston Hollow, was located in Yale Forest, Ashford, Tolland Co. The area includes a small, alternately rushing and swampy stream that runs between the steep bedrock walls of a ravine. At the ravine's south end a similar stream joins the outflow, and the combined streams flow into a series of swamps (Fig. 1).

The brook portions of the habitat contain mesic, mature deciduous forest dominated by yellow birch (*Betula lutea*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and an open understory of spicebush (*Lindera benzoin*) and black alder (*Ilex verticillata*). Swampy portions have a generally young canopy of hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), yellow birch, and red maple, and a dense understory of black alder, speckled alder (*Alnus rugosa*), and sweet pepperbush (*Clethra alnifolia*). The swamp at the south end of Boston Hollow is mainly deciduous, with a canopy largely composed of red maple.

I made limited observations at about 25 other sites throughout New England in addition to Boston Hollow. Observations from these sites were used to assess the generality of my findings at Boston Hollow.

Territoriality and banding. — I located territorial boundaries by recording the locations of song perches and territorial interactions. Territory size was determined with compass and tape measure. Additionally, I color banded adults for individual recognition, and weighed birds with a Pesola spring balance to ±0.1 g.

Foraging behavior. — In observing foraging, I noted the type of habitat used, the method of foraging, and the number of foraging activities. Based on Eaton's (1957, 1958) findings and my preliminary examinations, I divided waterthrush foraging sites into four categories: (1) water, (2) ground, (3) foliage, and (4) air. I separated each year's data into those collected before and after the leafing out of trees (about 10 May) because my preliminary observations indicated that habitat preference changed after leaf emergence in spring.

My observations also indicated that four general foraging methods occur: (1) picking, (2) leaf-pulling, (3) hawking, and (4) hovering. Of these, only leaf-pulling is uncommon among wood warblers (Bent 1953). It involves pulling dead leaves from litter or water with the bill and inspecting the revealed substrate or underside of the leaves for prey. For analysis of data on foraging methods, I again separated my observations into those collected before and after leaf emergence.

Invertebrate sampling. — I found that aquatic invertebrates predominated in the diet of waterthrushes, so I assessed prey availability only in the aquatic environment. During the study I sampled at eight different territories per species. Of these, two of the territories of Louisiana Waterthrushes overlapped with two of Northern Waterthrushes, but only 8% of the samples were from the zone of overlap.

I sampled each territory three times over the breeding season: (1) during incubation (mid-May), (2) during feeding of nestlings (early June), and (3) during feeding of fledglings (late June). Moreover, in 1980 I also sampled in late April to assess invertebrate biomass at the start of the breeding season.

Dip netting was used to sample because the technique caught benthic and swimming organisms, both of which waterthrushes eat. Although this method may have underestimated the number of fast-moving invertebrates, the results appeared to agree well with my visual estimates of the relative abundance of aquatic taxa. To sample I divided each territory into 10 "blocks" and then randomly selected a spot in each block. At each spot I submerged the net (9.5 × 7.5 cm; 16 meshes/cm) and moved it back and forth over 0.5 m for 10 sec. I then hand sorted samples, measured and identified specimens, stored specimens in 70% ethanol, and determined standardized wet weights (Craig 1981) of each sample.

I also established 11 size categories of prey, all but the first with a range of 3 mm (Table 1). The first, ≤4 mm, was mainly comprised of organisms nearly 4 mm in length, because organisms shorter than 3 mm could not be successfully removed from the samples. Organisms >19–22 mm were rare and consequently deleted from further analysis.

It was necessary to take many invertebrate samples because aquatic invertebrates are not distributed randomly (Southwood 1966). Because field time was divided between processing samples and observing bird behavior, insufficient time was available for sampling invertebrates in other habitats. However, the objective in studying prey was to compare the food of the two waterthrushes rather than to determine the absolute abundance of prey. If prey biomasses differ between the territories of the species, which are both closely associated with wetlands, I felt that such differences would most likely occur in the aquatic environment.

To determine whether the taxa in my invertebrate samples were the same as those actually taken by waterthrushes, whenever possible I recorded the type of prey the birds ate. Such data are incomplete, however, because it was often difficult to identify small prey.

TABLE 1

SIZE DISTRIBUTION OF INVERTEBRATE SAMPLES FROM WATERTHRUSH TERRITORIES

Species	Size class (mm)[a]						
	4	4–7	7–10	10–13	13–16	16–19	19–22
S. motacilla							
$\bar{x}$[b]	7.0	137.4	66.4	22.5	7.4	1.6	1.1
	±5.2	±62.1	±31.7	±6.9	±3.5	±1.3	±1.1
S. noveboracensis							
$\bar{x}$	5.1	150.4	77.8	24.6	2.1	<1	<1
	±4.3	±65.5	±70.0	±22.8	±1.6		

[a] Only those classes represented in most territories are included.
[b] Mean (±SD) number of individuals/sample, all three sampling dates combined.

Analysis.—To determine the overlap in feeding behavior between species I used the equation:

$$\text{Overlap} = 1 - 0.5 \, \Sigma \, |p_{x_i} - p_{y_i}|,$$

where p_x and p_y are the frequencies of resource use of species x and y, respectively, in category i (Schoener 1970). Abrams (1980) recommended this index because of its ease of computation and lack of a number of underlying assumptions.

RESULTS

Territoriality.—Territories of Louisiana Waterthrushes ($\bar{x} = 0.67$ ha, SD = ±0.35, N = 9), and Northern Waterthrushes ($\bar{x} = 0.47$ ha, SD = ± 0.26, N = 10) were not significantly different in size (Fig. 1). Of 27 waterthrush territories studied in Boston Hollow, 17 were overlapping. *Seiurus motacilla* territories overlapped from 73–100% of adjacent territories of *S. noveboracensis*. However, despite the overlap and occasional feeding of the species within a few meters of each other, they did not exhibit interspecific territoriality or appear to aggressively interact. In Cornwall, Connecticut, both species even built nests in the same upturned root (M. Root, pers. comm.). In contrast, both species were intensely aggressive toward conspecifics.

Weight.—Of 52 waterthrushes banded during this study, 14 *motacilla* and 19 *noveboracensis* were resident adults with comparable weights. I found little sexual difference in weight, but I did find that *motacilla* ($\bar{x} = 20.4$ g, SD = ± 0.88) was significantly heavier ($t = 16.6$, df = 31, $P < 0.01$) than *noveboracensis* ($\bar{x} = 16.1$ g, SD = ± 0.62).

Foraging.—When searching for prey, the two species exhibited similar behaviors. In aquatic foraging, birds typically alternated between wading and walking along logs, on branches, and at the water's edge, and they
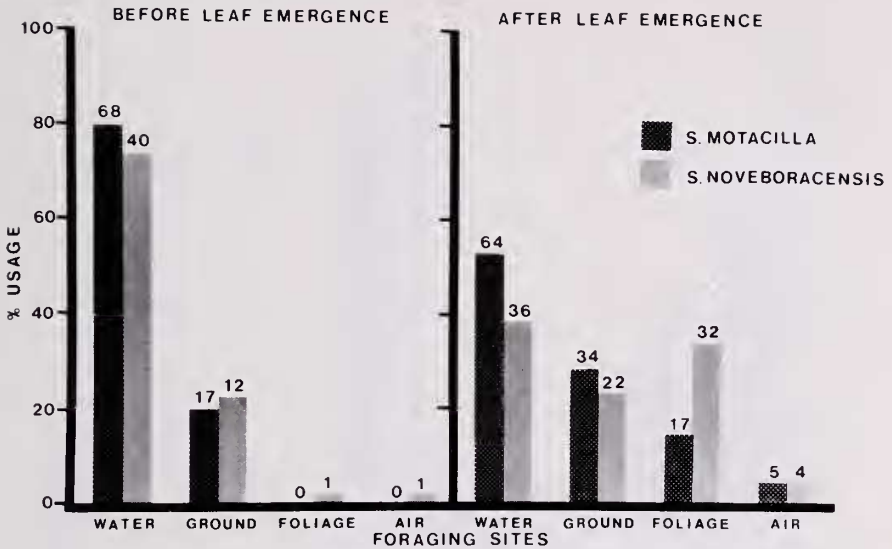
Fig. 2.   Use of foraging sites, based on data from 1978–1980. Numbers above bars represent total observations.

fed on both submerged and floating organisms. On a few occasions I watched birds flutter over the water to capture prey from its surface. Ground feeding included capturing prey on mud, in leaf litter, on rocks, and on moss. When feeding on woody plants, the birds walked on stout branches and picked prey from the foliage and stems with movements similar to those used for catching terrestrial prey.

Because picking did not occur in the air, hawking occurred only in the air, and leaf-pulling occurred only on the ground and in water, results for foraging methods mirror those of foraging sites to some extent. However, the categories involved in the two data sets are sufficiently distinct to warrant separate analysis. The two predominant foraging methods, picking and leaf-pulling, were used in both major foraging sites, the water and ground.

Comparison of pooled data on feeding sites revealed that both species made significant changes in their foraging sites after leafing out (*motacilla*: $\chi^2 = 22.4$, df = 2, N = 205, $P < 0.01$; *noveboracensis*: $\chi^2 = 24.6$, df = 2, N = 148, $P < 0.01$). Cumulative Chi-squares computed from individual year's data yielded similar results. The waterthrushes overwhelmingly fed in water early in spring, but although water remained an important feeding habitat, they also used other sites after leaf emergence (Fig. 2).

BEFORE LEAF EMERGENCE   AFTER LEAF EMERGENCE

% USAGE

100

80

60

40

20

0

142
70

S. MOTACILLA
S. NOVEBORACENSIS

24
40
33
10
0 1 2 2
9 5 5 4 8 10

PICK   PULL   HAWK   HOVER   PICK   PULL   HAWK   HOVER
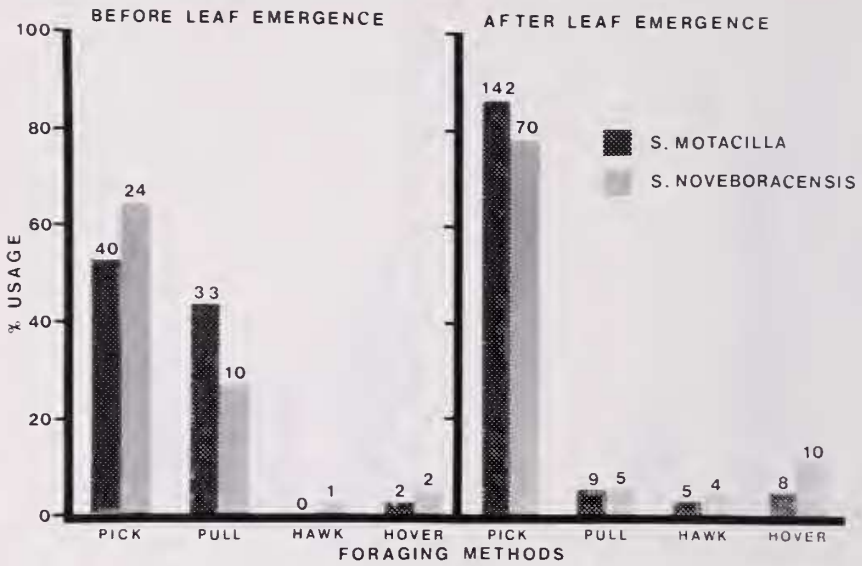FORAGING METHODS

FIG. 3. Use of foraging methods, based on data from 1978–1980. Numbers above bars represent total observations.

Pooled data also revealed that the two species foraged similarly prior to leafing out ($\chi^2 = 3.3$, df = 2, N = 139, $P > 0.05$), but diverged significantly afterwards ($\chi^2 = 12.1$, df = 3, N = 214, $P < 0.01$). Again, cumulative Chi-squares corroborate these findings. Northern Waterthrushes seemingly had a wider foraging range, using foliage, ground, and aquatic sites, whereas the Louisiana Waterthrushes used mostly ground and aquatic sites.

My comparison of pooled data on foraging methods revealed a change in behavior of the two species after leafing out (*motacilla*: $\chi^2 = 53.8$, df = 3, N = 239, $P < 0.01$; *noveboracensis*: $\chi^2 = 11.9$, df = 3, N = 126, $P < 0.01$), and cumulative Chi-squares were again in agreement. Before leafing out, both species used picking and leaf-pulling commonly, but afterwards picking clearly predominated. The frequency of leaf-pulling dropped sharply, and aerial foraging increased slightly for both species (Fig. 3). In contrast, analyses of pooled and annual data showed that the species did not significantly differ from each other in foraging methods (before leafing out: pooled $\chi^2 = 4.1$, df = 2, N = 112, $P > 0.05$; after leafing out: pooled $\chi^2 = 4.1$, df = 3, N = 253, $P > 0.05$).

The similarity between the species in their feeding behavior was reflected in overlap calculations. For the pooled data, use of foraging sites

TABLE 2

Taxonomic Composition of Invertebrate Samples from Territories of Waterthrushes

Taxon[a]	*S. motacilla*[b]	*S. noveboracensis*
Trichoptera	39.8 ± 29.7	9.4 ± 9.9
Ephemeroptera	40.0 ± 32.0	40.3 ± 46.6
Megaloptera	6.1 ± 6.9	5.1 ± 3.9
Diptera		
Miscellaneous	7.4 ± 5.4	14.4 ± 17.0
Chironomidae	103.4 ± 53.0	104.6 ± 98.6
Coleoptera		
Dytiscidae adult	4.4 ± 2.1	6.5 ± 5.1
Dytiscidae larvae	7.6 ± 6.5	10.8 ± 6.4
Helodidae	5.8 ± 11.0	5.9 ± 5.7
Isopoda	18.6 ± 11.7	16.3 ± 8.2
Oligochaeta	3.5 ± 2.3	5.9 ± 7.3
Gastropoda	2.3 ± 3.4	43.0 ± 34.8

[a] Only those taxa represented in most territories are included.
[b] Mean number of individuals/sample (±SD), all three sampling dates combined.

exhibited an overlap of 0.98 before and 0.92 after leaf emergence. For foraging methods the equivalent values were 0.83 before and 0.92 after leaf emergence.

Prey taken.—During my observations I could identify some types of prey captured by waterthrushes, particularly for *motacilla*. Because *motacilla* sometimes fed in more open sites, it was easier to observe than *noveboracensis*. Also, *motacilla* may take larger and therefore more easily identifiable prey, as discussed below. I saw *motacilla* eat the following types of aquatic organisms: isopods, gastropods, nymphs of Ephemeroptera, larvae of Trichoptera, larvae of Culicidae, and larvae of Dytiscidae. In addition, I observed birds feeding on terrestrial chilopods, lepidopteran larvae, adults of Culicidae, and unidentified emergent aquatic insects. *S. motacilla* ate organisms up to about 3 cm in length (centipede), and I saw individuals removing larvae of Trichoptera from their cases.

I could identify few prey taken by Northern Waterthrushes. Adults of Culicidae were eaten, and in late May both *noveboracensis* and *motacilla* ate caterpillars which were then emerging abundantly. These caterpillars were also fed to young. The largest item seen eaten by *noveboracensis* was about 1 cm long.

By turning wet leaves at waterthrush feeding sites in a manner analagous

TABLE 3

BIOMASS OF INVERTEBRATES FROM SAMPLES IN WATERTHRUSH TERRITORIES

Species	Sampling date		
	Mid-May[a]	Early June	Late June
S. motacilla	0.84 ± 0.64	0.77 ± 0.23	0.62 ± 0.52
S. noveboracensis	1.08 ± 0.51	0.53 ± 0.48	0.46 ± 0.19

[a] Mean (±SD) weight/sample (g).

to that used by waterthrushes, I found ready access to ephemeropteran nymphs and chironomid larvae. These observations, as well as my findings above, agree with Eaton's (1957, 1958) reports on types of aquatic prey eaten by waterthrushes.

Prey available.—Among 18 major invertebrate taxa found in my aquatic samples, Ephemeroptera and Chironomidae were most numerous (Table 2). There were significantly more Trichoptera ($t = 3.9$, df = 14, $P < 0.01$) and fewer Gastropoda ($t = 2.9$, df = 14, $P < 0.05$; log-transformed data) in *motacilla* than in *noveboracensis* territories.

By comparing percentiles, I found that territories of waterthrushes differed in only the upper 2% of their invertebrate size distributions ($t = 2.6$, df = 14, $P > 0.05$; log-transformed data). Thus, invertebrates > 13 mm occurred more frequently in territories of *motacilla* than in those of *noveboracensis*. Furthermore, territories of *motacilla* averaged 15% more than *noveboracensis* in biomass of invertebrates > 13 mm. The Trichoptera comprised 52% of the individuals > 13 mm in *motacilla* territories, which is 21% more than in *noveboracensis* territories.

No statistical differences between territories of the two waterthrushes ($F = 0.2$, df = 1, N = 2, $P > 0.05$; ANOVA) are reflected in analysis of invertebrate biomass (Table 3). I also detected no difference between the individual territories of each species ($F = 1.5$, df = 12, N = 16, $P > 0.05$; ANOVA). However, I did find a difference among the biomasses recorded on the three sampling dates ($F = 4.7$, df = 2, N = 3, $P < 0.05$; ANOVA). Biomass was highest early in the season (Duncan's test) and declined afterwards. The decline appeared steepest in territories of Northern Waterthrushes. A summer decline in invertebrate biomass is typical for small streams in the region (R. Pupedis, K. Thompson, pers. comm.), but an additional comparison of samples collected in late April, 1980 with early May samples did not differ ($t = 0.76$, df = 14, $P > 0.05$).

DISCUSSION

The two waterthrushes have usually been treated as ecologically distinct species, with *motacilla* associated with streams in deciduous woodland

and *noveboracensis* with swamps in coniferous forest (Bent 1953; Eaton 1957, 1958). Although these habitat preferences are generally true, my study clearly demonstrates that the waterthrushes can overlap in several respects.

Foraging of the two waterthrushes is similar, apparently overlapping to a greater degree than is the case in other closely related species (e.g., Schoener 1970, Voigts 1973). The similarity of habitat use in these species before leafing out may reflect the relatively high biomass of aquatic prey in that season. Differences after leafing out might be attributed to increased competition for a declining supply of aquatic prey, thus necessitating movement into alternate environments. This explanation, however, does not account for the remaining high overlap between the species.

Another explanation not dependent upon accounting for high overlap and lack of aggression between the species can be offered. Perhaps in the Pleistocene, separation of populations of an ancestral waterthrush occurred, such as is described for other Parulinae by Mengel (1964). These isolates might have evolved different behavioral traits facilitating foraging in different habitats. Divergence detected today might be a by-product of independent specialization of each species rather than a result of interspecific competition.

My data on foraging methods also demonstrate high overlap between the two species. The lack of significant differences suggests that differences in foraging do not serve to reduce competition between the two species. Thus, interspecific territoriality, divergence in foraging sites, and divergence in foraging methods do not appear to be involved in ecologically separating waterthrushes.

Invertebrate data do suggest that waterthrushes select breeding habitats with aquatic organisms of different size distributions. Larger insectivorous birds are known to eat larger prey than smaller but similarly feeding birds (Hespenheide 1973). However, it is not known if selection by *motacilla* of territories which contain an average of 15% more large organisms than in *noveboracensis* territories reduces competition between the two species.

I conclude that evidence for competition between the Louisiana and Northern waterthrushes is weak, despite their apparent similarity. This suggests that competition is not always a factor influencing use of resources by ecologically similar species. Rabenold (1978) suggested that, in the northeast, foliage invertebrates undergo a summer pulse in abundance so great that they are not in limited supply for predators. If this also occurs in prey consumed by waterthrushes, then competition need not occur, and foraging behavior of the species need not diverge. In addition, other as yet undetermined factors, such as those that might act to reduce waterthrush populations below equilibrium densities, may also be responsible for reducing the intensity of competition between these species.

SUMMARY

The territoriality, foraging behavior, and aquatic prey of breeding Louisiana (*Seiurus motacilla*) and Northern (*S. novaboracensis*) waterthrushes were studied in northeastern Connecticut. Although intensely aggressive toward conspecifics, the species had overlapping territories and were similar in both use of foraging sites and in methods of foraging. Few significant differences between territories of the two species occurred with respect to biomass, taxonomic composition, and size distribution of aquatic invertebrates. Despite similarity in behavior and in resource availability of their territories, evidence for interspecific competition between the species appeared weak. It is suggested that the waterthrushes coexist without competing because resources are not in limited supply, and that differences which do exist between the species have evolved in response to factors other than competition.

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